Call Characteristic Network Reveal Geographical Patterns of Call Similarity: Applying Network Analysis to Frog's Call Research

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Abstract Individual's phenotypic traits are the results of adaptation to ecological conditions. Therefore, different selection pressures caused by heterogeneous environments may result in phenotypic difference, especially for individuals in different geographical populations. Here, we illustrated for the first time to use social network analysis (SNA) for examining whether geographical proximity predicts the similarity patterns in call characteristics among populations of an anuran species. We recorded calls from 150 male dorsal-striped opposite-fingered treefrogs (*Chiromantis doriae*) at 11 populations in Hainan Province and one population in Guangdong Province in mainland China, and we measured eight acoustic variables for each male. Mantel test didn't show a correlation between geographical proximity and the similarity in call characteristics among populations. In addition, we failed to find correlations between a population's eigenvector centrality and the distance to its nearest neighbor, nor between the coefficient of variation of similarity in call characteristics of a population and the average distance to all other populations. Nevertheless, three acoustic clusters were identified by the Girvan-Newman algorithm, and clustering was partially associated with geography. Furthermore, the most central populations were included in the same cluster, but the top betweenness populations were located within different clusters, suggesting that centrality populations are not necessary bridging between clusters.

These results demonstrate the potential usefulness of the SNA toolbox and indicate that SNA helps to uncover the patterns that often overlooked in other analytical methods. By using SNA in frog's call studies, researchers could further uncover the potential relationship in call characteristics between geographical populations, further reveal the effects of ecological factors on call characteristics, and probably enhance our understanding of the adaptive evolution of acoustic signals.

1. Introduction

Individual's phenotypic traits are the results of adaptation to ecological conditions. Therefore, different selection pressures caused by heterogeneous environments may result in phenotypic differences of individuals in different geographical populations, including body size, coloration and diet (Roth *et al.*, 2007; Wilson *et al.*, 2013; Chirikova *et al.*, 2019). Recently, geographical variation in vocalization has been reported in some songbirds and mammals (Ey and Fischer, 2009; Ahonen *et al.*, 2014; Eisinger *et al.*, 2016; Branch and Pravosudov, 2019), which have large repertoires. In addition, vocal dialects may further form and maintain merely by geographic isolation, or due to local adaptation, acoustic adaptation or social adaptation that result from geographic isolation (MacDougall-Shackleton and MacDougall-Shackleton, 2001; Henry *et al.*, 2015; Casey *et al.*, 2018; Araya-Salas *et al.*, 2019).

In contrast to songbirds and mammals, the acoustic

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feature and call structure of anurans are relatively simple. Nevertheless, vocal communication plays crucial roles in sexual selection of most anurans (Gerhardt and Huber, 2002), and acoustic properties of the calls commonly convey information concerning a male's body conditions (Wang *et al.*, 2012; Ziegler *et al.*, 2016) or its resource qualities (Cui *et al.*, 2012). Thus, investigating the variation in vocalization of anurans between geographical populations may help to understand the evolution of sexual signals (Gerhardt, 1994; Trillo *et al.*, 2013; Velasquez, 2014).

In the present study, we illustrated the application of social network analysis (SNA) for investigating the geographical patterns in call characteristics of dorsal-striped opposite-fingered treefrogs (*Chiromantis doriae*). SNA has been widely applied in animal behavior research (Krause *et al.*, 2007; Kurvers *et al.*, 2014; Farine and Whitehead, 2015; Croft *et al.*, 2016). This analytical tool provides specific network metrics that allow researchers to quantify social associations between individuals (Deng *et al.*, 2017; Qi *et al.*, 2017; Xia *et al.*, 2019), elucidate the links between individual behavior and population-level dynamic patterns (de Silva *et al.*, 2011; Pinter-Wollman *et al.*, 2014) as well as track the spread of information or disease through a population (Farine, 2017; Fountain-Jones *et al.*, 2017; Silk *et al.*, 2018). In fact, SNA not only can be used to quantify various social interactions (Morueta-Holme *et al.*, 2016; Sabol *et al.*, 2018; Deng and Cui, 2019; Meise *et al.*, 2019), but also any shared property between pairs (Weiss *et al.*, 2014; Potvin *et al.*, 2019).

Here, we used both traditional methods and SNA to investigate the geographical patterns of call similarity. Firstly, we aimed to examine whether geographical proximity (based on geographical coordinates of the recording site) predicts the similarity of call characteristics of *C. doriae* between populations. Secondly, we attempted to describe the patterns of clusters in a network of call characteristics. Thirdly, we investigated whether geographical location influences call characteristic network structure. By doing this, we will gain understanding about the geographical patterns of call similarity.

2. Materials and Methods

2.1. Acoustic data We recorded 745 calls from 150 male dorsal-striped opposite-fingered treefrogs in 3 years (2015–2017) at 11 populations in Hainan Province and one population in Guangdong Province in mainland China (Table 1). For each male, three to five calls were recorded using a digital voice recorder (Marantz PMD 661) connected to a directional microphone (Sennheiser ME66 with K6 power module). We measured the following eight acoustic variables: call duration, notes per call, call rate, call interval, dominant frequency, high frequency, low frequency and modulation range (Figure 1). The

Table 1 Locations, geographic coordinates, and number of recorded males of *Chiromantis doriae* analyzed in this study.

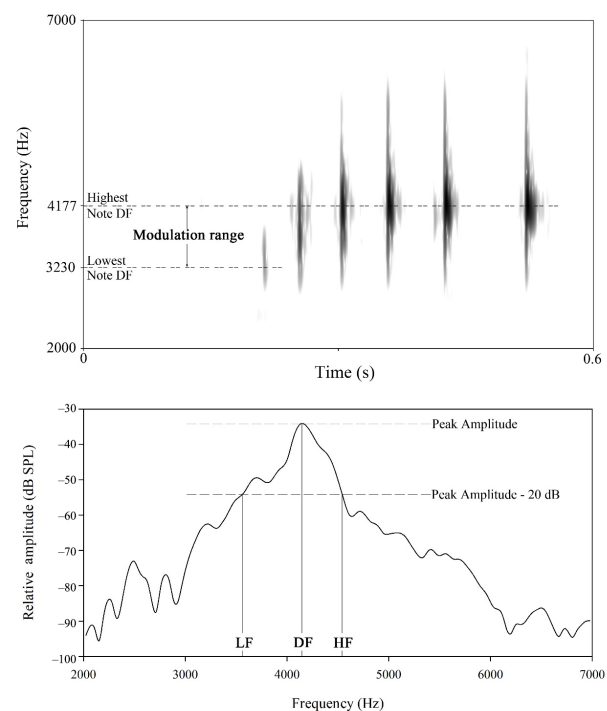| Location	Latitude	Longitude	Sample size
Zhanjiang	20.28° N	110.22° E	7
Danzhou	19.70° N	109.23° E	10
Ding'an	19.67° N	110.34° E	6
Chongshan	18.79° N	109.51° E	17
Ledong	18.56° N	109.08° E	13
Lingshui	18.66° N	109.93° E	11
Dongfang	19.12° N	108.80° E	17
Sanya	18.34° N	109.52° E	12
Wanning	18.92° N	110.32° E	14
Shuiman	18.88° N	109.67° E	19
Diaoluo	18.72° N	109.87° E	16
Huangzhu	19.44° N	110.40° E	8

Figure 1 A subset of the acoustic variables of *Chiromantis doriae* measured in this study. DF: dominant frequency; HF: high frequency; LF: low frequency.

dominant frequency, low frequency and high frequency of the calls were obtained using PRAAT software, and other variables were obtained using Adobe Audition 3.0 software (California, USA). For each acoustic variable, we averaged over individual the measurements obtained. We used principal component analysis (PCA) to reduce dimensions and eliminate collinearity of acoustic variables. We used the squared Mahalanobis distance among populations, calculated using principal component of acoustic variables in HDMD package (McFerrin, 2013), as a measure of similarity in call characteristics among

populations (Yoktan *et al.*, 2011). Mahalanobis distance is based on correlations between principal components, and a shorter distance implies closer resemblance between call profiles from different populations.

2.2. Quantifying network measure We used the inversely transformed squared Mahalanobis distances to generate network, and thus the larger distance represented more similar call characteristics between populations. We used the Girvan-Newman algorithm (Girvan and Newman, 2002) to define clusters in a network, and modularity (Q) to find the most fitted number of clusters (Newman and Girvan, 2004). We found that the cluster structure associated with the highest Q value when using the first principal component of acoustic variables to calculate the squared Mahalanobis distance. We calculated eigenvector centrality, betweenness and the coefficient of variation (CV) of similarity in call characteristics for each population. Eigenvector centrality is based on the sum of the centralities of an individual's neighbors (Farine and Whitehead, 2015), and it quantifies how similar each population's call characteristics is overall relative to all other populations. Betweenness is based on the count of the number of shortest paths that flow through a given individual (Farine and Whitehead, 2015), and populations with a high betweenness are likely to connect largely independent clusters. The CV of similarity measures how varied similarity is among populations, and a higher CV value indicates relatively stronger variation in similarity with others (Whitehead, 2008). All network calculations were performed using the IGRAPH package (Csárdi and Nepusz, 2006).

2.3 Statistical analysis To test whether geographical proximity (based on GPS coordinates of the recording site) predicts the similarity in call characteristic among populations, a Mantel test with 9999 permutations was performed using ADE4 package. To explore whether geographical proximity predicts how similar a population is to all others, we estimated the correlation (Pearson) between eigenvector centrality and the distance to its nearest neighbor. To explore whether geographical proximity predict how varied similarity is among populations, we estimated the correlation between the CV of similarity in call characteristics of a population and the average distance to all other populations. We constructed 1000 random networks, and then calculated eigenvector centrality and CV value and conducted the same analysis for each permuted network that we did for the observed data. *P*-values were calculated by comparing the coefficient from correlation analysis based on the observed data with the coefficient from the same analysis based on the randomized data. A result was considered significant if the observed coefficient fell outside the 95% range of the random coefficient distribution. All statistical analyses were performed using R software (R Core Team, 2016).

3. Results

The PCA analysis revealed that 3 components from the original 8 acoustic variables accounted for 74% of the variation (Table 2). The first component (explained 30% of variance) had high positive loading scores for three spectral parameters: dominant frequency, high frequency and low frequency. The second (explained 27% of variance) and the third component (explained 17% of variance) mainly represented the temporal parameters (Table 2).

Table 2 Factor loadings of the principal component analysis on the acoustic variables of *Chiromantis doriae*. Absolute values higher than 0.6 are shown in bold.

Acoustic variables	RC1	RC2	RC3
Dominant frequency	**0.95**	−0.21	−0.03
High frequency	**0.76**	−0.49	0.00
Low frequency	**0.91**	0.21	−0.07
Call length	−0.23	**0.90**	0.11
Note number	−0.10	**0.78**	−0.03
Note range	−0.09	**−0.63**	0.26
Call rate	0.04	0.15	**−0.79**
Call interval	−0.02	0.03	**0.82**
Proportion variance (%)	30	27	17
Cumulative variance (%)	30	57	74

Mantel test revealed that there was no significant correlation between geographical proximity and pairwise Mahalanobis distances ($r = -0.036$, $P = 0.591$). We constructed a network based on the squared Mahalanobis distance of the first principal component of acoustic variables between populations, and we identified 3 clusters on the network (Figure 2). Firstly, clustering was partially associated with geography. The smallest cluster included 2 populations in the southeastern region of Hainan, and the two largest clusters each included 5 populations mainly in the central or in the northwestern region. Secondly, the most central populations in this network were Wanning and Lingshui, which were located within the same cluster (Figure 2A). Ding'an and Huangzhu had the highest betweenness, each of which was located within a different cluster (Figure 2B). Lastly, we did not find a relationship between a population's centrality and the distance to its nearest neighbor in the network ($r = 0.097$, $P = 0.631$, Figure 3A), nor between the CV of similarity in call characteristics of a population and the average distance to all others ($r = -0.052$, $P = 0.460$, Figure 3B).

4. Discussion

Geographical variation among populations in acoustic signals has been documented in various taxa (Zuk *et al.*, 2001; Lameira

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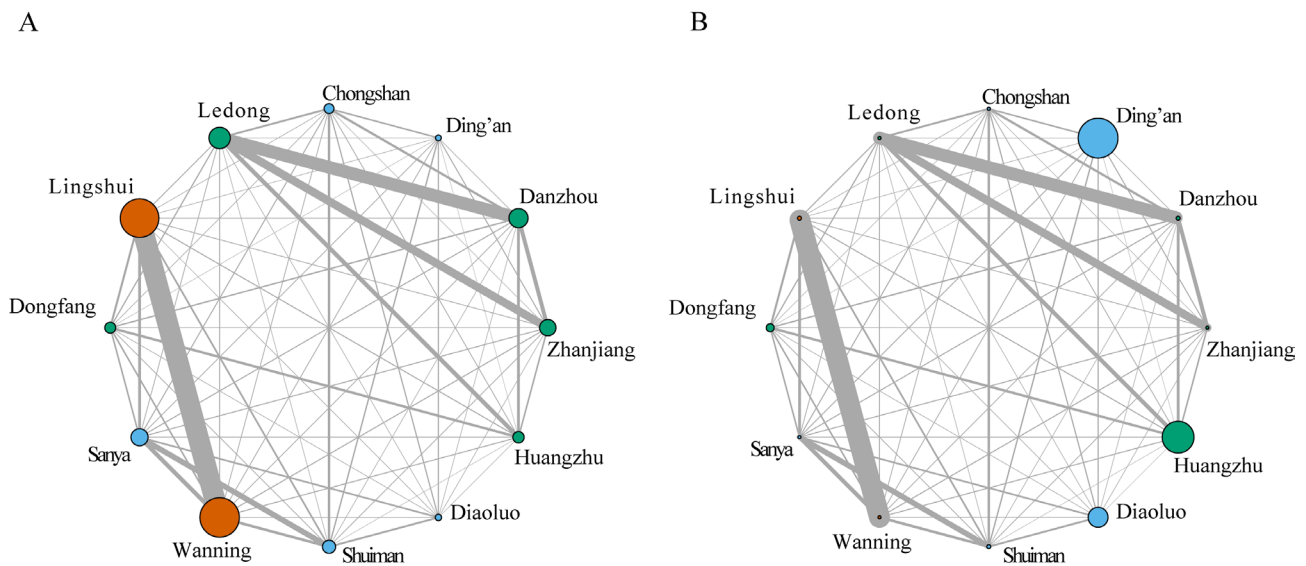in a Treefrog

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Figure 2 Call characteristic network based on the squared Mahalanobis distance between populations. Nodes are colored by cluster identified by the Girvan and Newman (2002) algorithm and sized by their eigenvector centrality (A) or betweenness (B). Thickness of edges represents the similarity in call characteristics between populations.
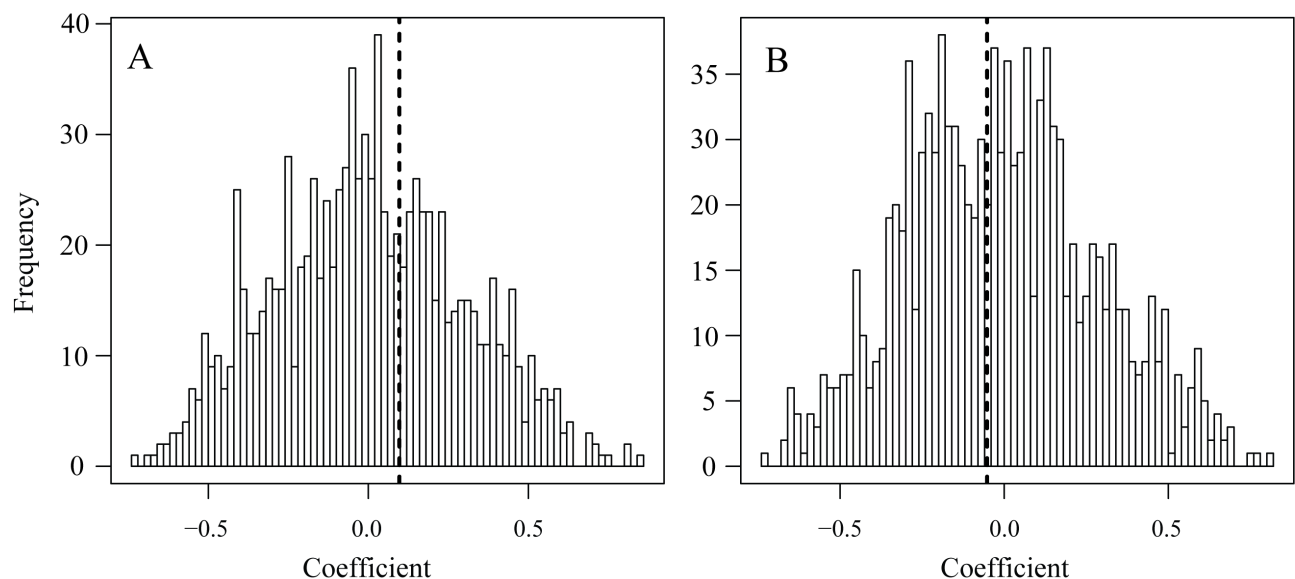

Figure 3 Comparison of the coefficient from correlation analysis based on the observed data (dashed vertical line) and the frequency distribution of coefficient from the same analysis based on randomized data: (A) eigenvector centrality, (B) coefficient of variation.

et al., 2010; Velasquez, 2014), and the study of intraspecific variation of call characteristics is important for understanding the origin of divergence in vocal communications and even the species divergence. In this study, we investigated the geographical patterns in call characteristics of *C. doriae* using both Mantel tests and social network analysis. We failed to find a correlation between geographical proximity and the similarity in call characteristics among populations, though the variations of call characteristics related to geographical

distance among populations have been reported in some studies (Bernal *et al.*, 2005; Pröhl *et al.*, 2007). Our result is in line with that of Velásquez et al. (2013), who reported that the bioacoustic distances among different populations of four-eyed frog (*Pleurodema thaul*) were not correlated with geographical distances. Similarly, a study on Alpine marmots (*Marmota marmota*) found differences in the acoustic structure of the alarm calls among populations, but these differences could not be explained by geographical distances (Lengagne *et al.*, 2020).

These contrasting results imply that the geographical proximity may not be a necessary indicator for the variations of call characteristics among populations.

With our limited data, however, the visualized call characteristic networks did show some patterns (Figure 2). Three acoustic clusters were identified by the Girvan-Newman algorithm, and clustering was partially associated with geography. In addition, we found that the two most central populations formed a cluster. According to the definition of eigenvector centrality, the call characteristics of these two populations were most similar to those of all other populations. Furthermore, high centrality populations can be viewed as call distributors, which indicate that they might possess the original call characteristics of this species. We also found that the top betweenness populations were located within different clusters, suggesting that centrality populations are not necessary bridging between clusters. Generally, higher betweenness implies a location that provides a bridge between other individuals. In the present study, the top betweenness populations were not located in the central of the geographical region, implying that the geographical patterns of call similarity might be influenced by other factors, such as geographic barriers, selection pressure and local environments. Overall, these results indicate that SNA helps to uncover the patterns that often overlooked in other analytical methods.

However, our data did not show correlations between geographical proximity and a population's eigenvector centrality or the CV of similarity in call characteristics of *C. doriae*. Similar results could be found in the studies on spatial distribution of dialect in songbirds. For example, Yoktan *et al.* (2011) reported that the variance among song dialects in orange-tufted sunbird (*Nectarinia osea*) could poorly be explained by settlement establishment date, geographical position, or genetic distance between populations. Nevertheless, SNA results showed that dialects seemed to aggregate into several clusters, and the dialect clusters were partially associated with geography, which suggested that historical processes may have played a role in the formation of dialect clusters (Yoktan *et al.*, 2011). In addition, Potvin *et al.* (2019) applied SNA techniques to investigate song sharing between silvereyes (*Zosterops lateralis*) populations. They found that geographical proximity could not explain the centrality of a population or song similarity between populations, though the network of syllables from the 19 populations presented moderate clustering (Potvin *et al.*, 2019). In the present study, the possible explanations are relatively small spatial scale and relatively younger population establishment time of *C. doriae* according to the divergence times of the genus *Chiromantis* (Li *et al.*, 2013), because many studies on anurans have shown that male advertisement call characteristics display phylogenetic signal (Goicoechea *et al.*,

2010; Gingras *et al.*, 2013; McLean *et al.*, 2013; Sosa-Lopez *et al.*, 2016).

The primary objective of this study is to explore the use of SNA in the geographical patterns in call characteristics of a treefrog, and our results demonstrate the potential usefulness of the SNA toolbox. Most studies on frog's call have focused on the differentiation in call characteristics between sympatric related species (Liu *et al.*, 2018; Chen *et al.*, 2020) and the effects of ecological factors on the call structures (Trillo *et al.*, 2013; Narins and Meenderink, 2014; Goutte *et al.*, 2018). Combined with SNA techniques, researchers could increase the usefulness of the data, further uncover the potential relationship in call characteristics between geographical populations, and probably enhance our understanding of the adaptive evolution of acoustic signals.

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